THE FIRST ZOEAL STAGES OF *CANCER PAGURUS* L., *PINNOTHERES PISUM* (PENNANT) AND *MACROPHTHALMUS DEPRESSUS* RÜPPELL (CRUSTACEA, DECAPODA, BRACHYURA).

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SYNOPSIS

The first zoeal stages in *Cancer pagurus*, *Pinnotheres pisum* and *Macrophthalmus depressus* are described and larval characters within their respective families are discussed.

INTRODUCTION

ALTHOUGH there are published accounts of one or more larval stages of several hundreds of brachyuran species, less than one hundred of these descriptions include a significant amount of detail. Consequently, while there has been a welcome tendency in recent years for larval papers to deal with all the developmental stages of crabs reared in the laboratory, there is still a need for detailed re-descriptions, even of single zoeal stages, where the previous accounts are clearly inadequate. The purpose of this paper is to provide such details of the first zoeal stages of three crabs from material in the larval collections of the British Museum (Natural History).

Cancer pagurus

Larvae hatched from a female collected at Lulworth Cove, Dorset, June, 1973. B.M.(N.H.) registration no. 1975 : 66.

Dimensions : Tip of dorsal to tip of rostral spines : 2·4–2·6 mm.
Tip to tip of lateral carapace spines : 1·0–1·1 mm.

Carapace (Fig. 1a, b) :

Dorsal carapace spine straight or with a very slight backward curve, about twice as long as the carapace and slightly longer than the straight rostral spine. Rostral spine with minute spinules. Lateral spines about half carapace length. Carapace with a low anterio-median papilla, a pair of setae at the base of the dorsal spine and posterio-lateral margins without sub-marginal setae.

Antennule : Simple, with 2 or 3 aesthetascs and a single seta.

Antenna (Fig. 1c) : Spinous process slightly more than half length of rostrum, with spinules on the distal two-thirds increasing in size towards the tip. Exopod about one-third length of spinous process, with 1 long terminal seta and 2 shorter ones, of which 1 is fused.

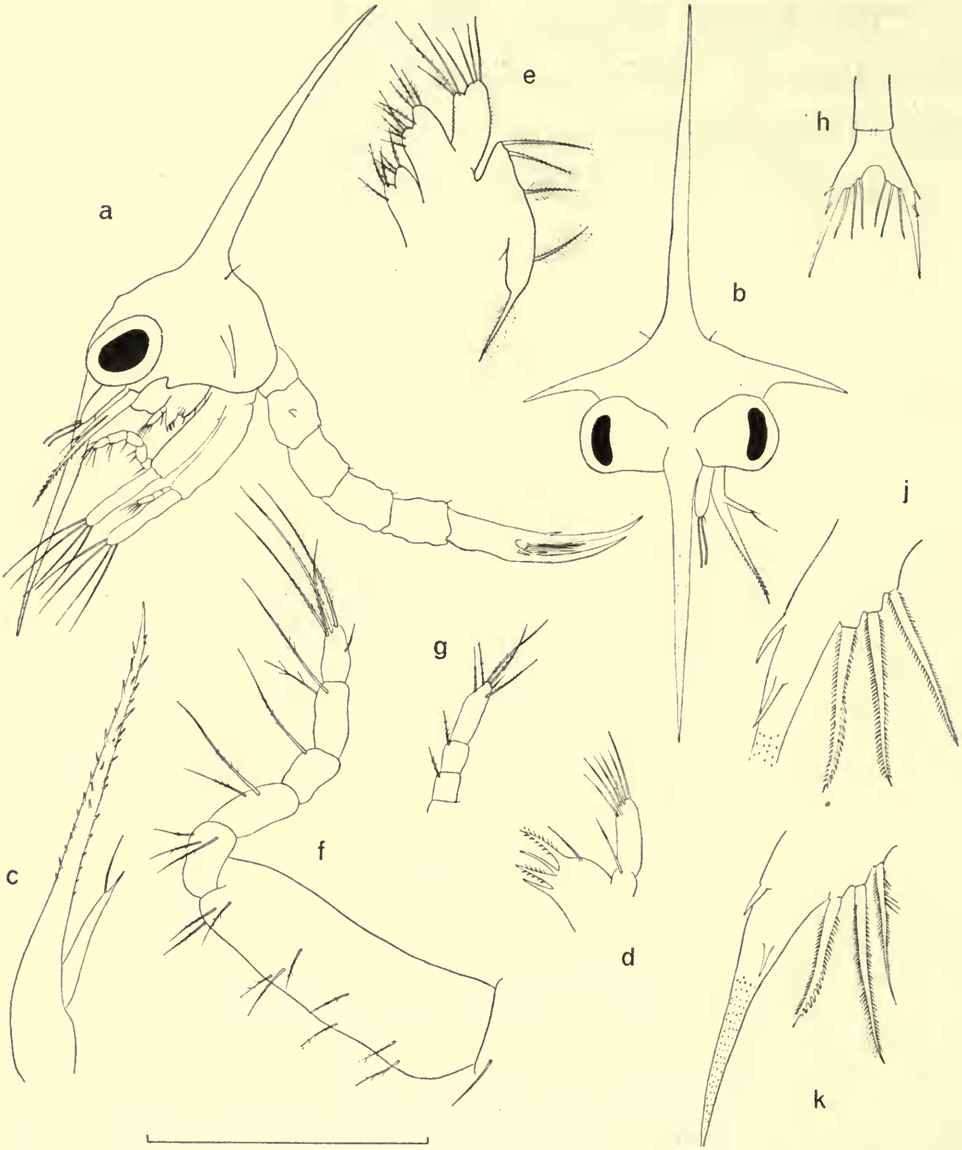

FIG. 1. *Cancer pagurus*, first zoea: a, lateral view; b, frontal view; c, antenna; d, maxillule; e, maxilla; f, first maxilliped (exopod omitted); g, endopod of second maxilliped; h, telson; j, detail of telson; k, detail of telson in the third zoea of *C. anthonyi*. Bar scale represents 0·5 mm for a, b and h, and 0·25 mm for c–g, j and k.

Maxillule (Fig. 1d): Endopod of 2 segments, with 1 and 6 setae respectively.
Maxilla (Fig. 1e): Endopod bilobed with 3+5 (occasionally 4) setae; scaphognathite with 4 marginal setae and a long plumose posterior projection.

First maxilliped (Fig. 1f) : Basis with 10 setae (arranged 2, 2, 3, 3) ; endopod segments with 3, 2, 1, 2 and 4+1 setae ; exopod with 4 natatory setae.
Second maxilliped (Fig. 1g) : Basis with 4 setae ; endopod of 3 segments with 1, 1 and 6 setae.
Abdomen (Fig. 1a) : Somite 2 with forwardly directed dorso-lateral knobs ; somites 2–5 each with a pair of dorso-posterior setae and slight projections on the posterio-lateral margins.
Telson (Fig. 1h, j) : Forks long, slender and divergent, each with one lateral and one dorsal spine, and minute spinules distally ; inner posterior margin with a deep, rounded median notch and three pairs of processes armed with short setules and spinules, those of the distal one-third of the outer process being particularly stout and tooth-like.

DISCUSSION.

The larvae of *Cancer pagurus* were first hatched by Thompson in 1829 and have subsequently been described many times (see Lebour, 1928a). However, with the exception of Williamson's (1910) account, most of these descriptions are very inadequate and the larvae of several Pacific species of the genus are much better known than are those of *C. pagurus*. Thus, Aikawa (1937) published details, including appendage setation, of the first stage of *C. gibbosulus* (de Haan), Mir (1961) compared the first zoeae of *C. magister* Dana, *C. antennarius* Stimpson and *C. anthonyi* Rathbun, Poole (1966) described the complete development of *C. magister*, and Trask (1970, 1974) has similarly dealt with *C. productus* Randall and *C. anthonyi*. From these accounts, including the details of *C. pagurus* given here, it is now possible to define generic, and possibly familial, zoeal characters.

All of the *Cancer* zoeae so far known possess well-developed dorsal, rostral and lateral carapace spines, antennae with spinous processes more than half as long as the rostrum, the two-segmented endopod of the maxillule with 1+4 to 1+6 setae, the endopod of the maxilla with at least six setae, usually arranged in two distinct groups, lateral knobs on only the second abdominal somite and the telson furcae with one lateral and one dorsal spine. In all the species, with the exception of *C. anthonyi*, the proximal segment of the endopod of the first maxilliped is described as carrying three setae and this, together with the characters listed above, distinguishes these *Cancer* zoeae from those of all other known brachyurans. Mir also recorded three setae on this segment in his first-stage *C. anthonyi* but Trask (1974) reported only two setae in all five stages of his reared material. This character seems generally to be rather conservative amongst brachyuran zoeae, at least within genera* and often within whole families, so that it seemed at least possible that Trask was mistaken. However, I have been able to examine Trask's material and can confirm that *C. anthonyi* does differ from the other known species in this respect. But this species possesses the strong tooth-like spines on the outer posterior telson process (see Fig. 1j, k) which seem to be typical of *Cancer* zoeae and which have

* For instance, a re-examination of the material of *Corystes cassivelaunus* described by Ingle & Rice (1971) revealed that the first zoea carries three setae on this segment, as in the later stages, and not two as figured in that paper.

otherwise been reported only in the closely related *Atelecyclus rotundatus* (Olivi) (Bourdillon-Casanova, 1960).

Pinnotheres pisum (Pennant)

Larvae hatched in July, 1971, from a female collected at Plymouth, Devon.

B.M.(N.H.) registration no. 1975 : 67.

Dimensions : Tip of rostral spine to mid-dorsal point of the carapace : 0·60 mm.
Tip to tip of lateral carapace spines : 0·55 mm.

Carapace (Fig. 2a, b) :

Rostral spine about half carapace length, with a slight forward curve. Lateral spines arise close to the posterio-lateral carapace margins, directed downwards and slightly backwards. No dorsal spine, but with a pair of setae close to the mid-dorsal line of the carapace.

Antennule (Fig. 2d) : Reduced to small hemispherical buds carrying 2 aesthetascs and a single seta.

Antenna : Totally absent.

Maxillule (Fig. 2e) : Endopod of two segments carrying 0 and 5 setae respectively.

Maxilla (Fig. 2f) : Coxal and basal endites not clearly bilobed ; endopod with 3 setae, of which 2 are more or less terminal ; scaphognathites with 3 marginal setae and a long plumose posterior process.

First maxilliped (Fig. 2g) : Basis with 2, 2, 3, 3 setae ; endopod segments with 2, 2, 1, 2 and 4+1 respectively ; exopod with 4 natatory setae.

Second maxilliped (Fig. 2h) : Basis with 4 setae ; endopod of 2 segments with 0 and 4 or 5 setae ; exopod with 4 natatory setae.

Abdomen (Fig. 2c) : Somites 2 and 3 with small dorso-lateral knobs, those of the second somite joined by a slight ridge over the dorsal surface. Somites 4 and 5 widening to the tri-lobed telson ; rounded median lobe not protruding beyond the acute lateral lobes ; three setose processes between the median and lateral lobes on each side.

Discussion.

Lebour (1928a, b) described the first stage of *P. pisum* hatched from the egg and attributed to the same species a second-stage zoea taken in the plankton. Her description is very inadequate, but where comparison is possible it agrees with that given here except that Lebour was able to detect the rudimentary antenna and found the median telson lobe to overreach the lateral lobes.

The available descriptions of the larvae of other species of *Pinnotheres* indicate that there is a good deal of morphological variation within the genus. Thus, while the zoeae of *P. pinnotheres* (L.) (= *veterum*) and *P. maculatus* Say possess dorsal, rostral and lateral carapace spines (see Hyman, 1925 ; Labour, 1928a, b ; Costlow & Bookhout, 1966), the dorsal spine is absent in *P. pisum* and *P. placunae* (Hornell and Southwell) (Lebour, 1928a, b ; Hashmi, 1970 ; this paper), the laterals are absent in *P. taylori* Rathbun (Hart, 1935), while none of the carapace spines are present in *P. ostreum* (Say) (Hyman, 1925 ; Sandoz & Hopkins, 1947). Similarly,

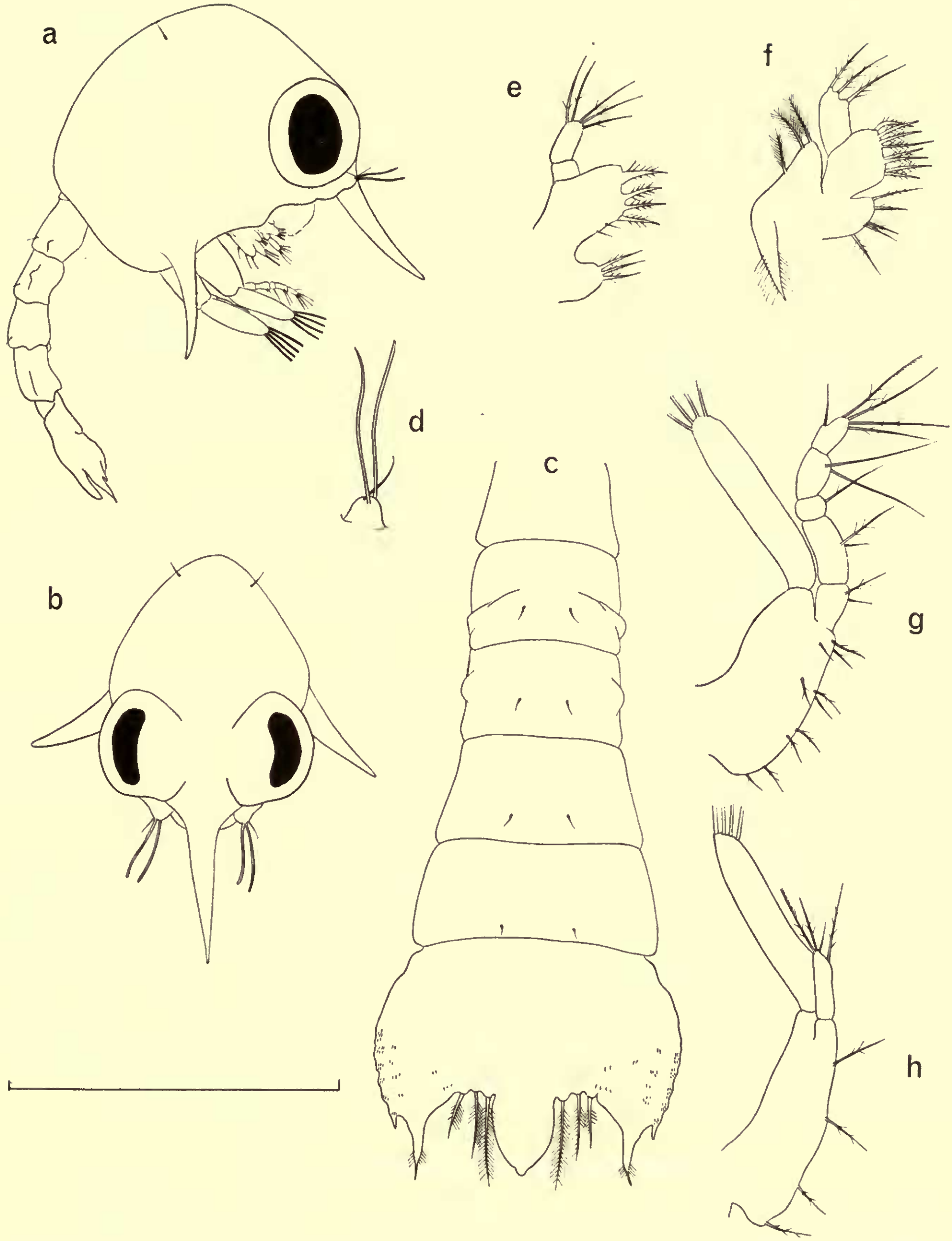

FIG. 2. *Pinnotheres pisum*, first zoea: a, lateral view; b, frontal view; c, abdomen; d, antennule; e, maxillule; f, maxilla; g, first maxilliped; h, second maxilliped. Bar scale represents 0·5 mm for a and b, and 0·25 mm for c–h.

while *P. pisum*, *P. pinnotheres*, *P. placunae* and *P. ostreum* possess the very characteristic trilobed telson which has been found only in the Pinnotheridae, in *P. maculatus* and *P. taylori* the telson is the much more typical brachyuran forked type. The degree of development of the antennules and antennae is also very variable, these appendages being greatly reduced or even absent, at least in the early stages, in *P. ostreum*, *P. placunae* and *P. pisum*, moderately developed in *P. taylori*, and quite normal in *P. maculatus*. The number of zoeal stages also varies within the genus, with *P. pinnotheres* and *P. taylori* having only two zoeae, *P. placunae* probably having three, *P. ostreum* four and *P. maculatus* five. One result of this variation in development rate is that the pleopods make their appearance at different stages in the different species, these appendages appearing as buds in the third stage in *P. ostreum* and the fourth in *P. maculatus*, but being well developed by the third stage in *P. placunae* or even as early as the second stage in *P. pinnotheres* and *P. taylori*. Finally, as Costlow & Bookhout (1966) point out, *P. maculatus* seems to have a far more typically 'brachyuran' development than any of the other described species, since it is apparently the only one in which the sixth abdominal somite is separated from the telson in the late zoeal stages.

Clearly, then, there is no difficulty in distinguishing between the known zoeae larvae of *Pinnotheres* species. A more difficult problem may be the recognition of characters common to the zoeae of *Pinnotheres* or of the Pinnotheridae generally, which will distinguish them from other crab larvae even where, as in *P. taylori*, neither the characteristic trilobed telson nor the posterio-ventrally directed lateral carapace spines are present.

Firstly, in all those species for which the information is available the endopod of the maxilla carries only three setae and these are arranged in a single more or less terminal group, or at least not clearly divided into two distinct groups. This character at once distinguishes the Pinnotheridae from almost all other brachyuran larvae, for such a setal armature has been recorded outside this family only in the Leucosiidae and the ocypodid sub-family Ocypodinae (see also below).

The three-segmented endopod of the second maxilliped readily distinguishes these ocypodids from both the Leucosiids and the pinnotherids in which this endopod never has more than two joints. Finally, while there are a number of differences between the pinnotherids and the leucosiids in the detailed morphology of the appendages, the most obvious distinction is the simple triangular telson with the closely spaced row of six processes on the relatively straight posterior margin which has been found in every leucosiid zoea so far described ; this contrasts strongly with both the tri-lobed telson and the more typical fork found in the Pinnotheridae.

Macrophthalmus depressus Rüpell

Larvae hatched in Bahrain, Arabian Gulf, from a female collected from the foreshore at Jufair in March, 1974.

B.M.(N.H.) registration no. 1975 : 68.

Dimensions : Tip of dorsal to tip of rostral spines : 0·66 m·m.
Maximum width across carapace : 0·29 mm.

Carapace (Fig. 3a, b) :

Slender dorsal and rostral spines, each about half the carapace length ; lateral spines absent. A pair of short setae at the base of the dorsal spine. Posterio-ventral edge of carapace with a small tooth and a slightly crenulate margin, but without sub-marginal setae.

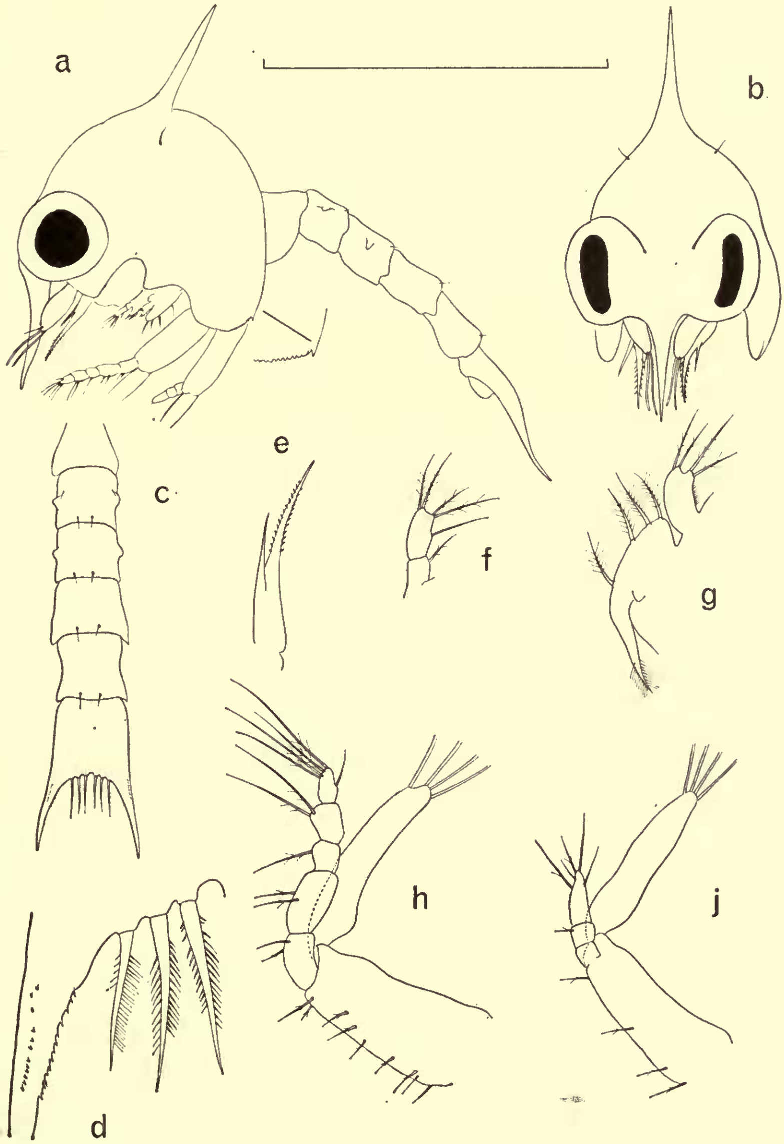

FIG. 3. *Macrophthalmus depressus*, first zoea : a, lateral view ; b, frontal view ; c, abdomen ; d, detail of telson ; e, antenna ; f, endopod of maxillule ; g, maxilla ; h, first maxilliped ; j, second maxilliped. Bar scale represents 0·5 mm for a–c, 0·25 mm for e–j, and 0·1 mm for d.

Antennule (Fig. 3b) : Simple, with 2 terminal aesthetascs and 1 seta.
Antenna (Fig. 3e) : Spinous process slightly shorter than rostrum ; exopod a simple, unarmed spine slightly more than half the spinous process.
Maxillule (Fig. 3f) : Endopod of 2 segments with 1 and 5 setae respectively.
Maxilla (Fig. 3g) : Endopod with 2 + 2 setae ; scaphognathite with 4 marginal setae and a long, plumose posterior process.
First maxilliped (Fig. 3h) : Basis with 9 or 10 setae ; endopod segments with 2, 2, 1, 2 and 4 + 1 setae ; exopod with 4 natatory setae.
Second maxilliped (Fig. 3j) : Basis with 4 setae ; endopod of 3 segments with 0, 1 and 5 setae respectively ; exopod with 4 natatory setae.
Abdomen (Fig. 3c) : Somites 2 and 3 with dorso-lateral knobs ; somites 2–5 each with short posterio-lateral processes and a pair of short setae close to the dorso-posterior margin. Telson widening only slightly posteriorly, the forks about the same length as the body of the telson. Posterior margin with three pairs of process which are naked distally (see Fig. 3d). Telson forks unarmed except for two rows of minute spinnules basally.

Discussion.

Hashmi (1969) described the first zoeae of five species of *Macrophthalmus*, including *M. depressus*. In general, Hashmi's account agrees very closely with that given here, except in the details of the setation of the maxillipeds. For instance, Hashmi gives the setal formula of the endopod of the first maxilliped as 1, 2, 1, 2, 5, whereas with the exception of his own account of *M. crinitus* Rathbun and the larvae of *Dotilla blanfordi* Alcock and *D. sulcata* (Forskäl) (Rajabai, 1959 ; Ramadan, 1940) the proximal segment carries two setae in every ocypodid larva for which this information is known, and the typical setal formula for the family seems to be 2, 2, 1, 2, 5.

Similarly, Hashmi records a seta on the basal segment of the endopod of the second maxilliped whereas I was unable to find a seta in this position in my material and it seems to be unusual in the family as a whole (Table 1).

Using characters of the carapace spines, antennae, telson, maxillae and maxillipeds Aikawa (1937) was able to separate zoeae of the ocypodid genera *Macrophthalmus*, *Tympanomerus* (= *Ilyoplax*), *Scopimera* and *Uca* into groups corresponding to the three sub-families based an adult taxonomy. Thirty years later Wear (1968) re-examined the larval situation within the Ocypodidae, information on the larvae of fourteen species belonging to seven genera by then being available, but was unable to obtain any support for the adult classification. However, in separating the larvae into groups Wear gave greatest significance to the presence or absence of lateral carapace spines, and somewhat lesser significance to the form of the abdomen and the degree of development of the antennal exopod. There is, however, a good deal of evidence to suggest that the setation of the mouthparts may reflect taxonomic divisions between larvae more effectively than these more 'obvious' characters. Certainly, on the basis of the setation of the endopods of the maxillules, maxillae and of the second maxillipeds the described ocypodid larvae fall into distinct groups, which correspond rather well with the accepted sub-families (Table 1).

TABLE 1

Setation of the maxillae and the second maxilliped, the number of telson fork spines, and the presence or absence of lateral carapace spines in described ocypodid zoeae

	Maxillule endopod	Maxilla endopod	Maxilliped 2 endopod	Telson fork spines	Lateral carapace spines	Source
MACROPHTHALMINAE						
Macrophthalmus depressus	1, 5	2, 2 (4)	0, 1, 5	0	–	This paper
Macrophthalmus depressus	1, 5	2, 2 (4)	1, 1, 5	0	–	Hashmi, 1969
Macrophthalmus depressus	1, 6	2, 2 (4)	1, 1, 6	0	–	Aikawa, 1929
Macrophthalmus dilatatus	1, 5	2, 2 (4)	1, 1, 6	0	–	Aikawa, 1929
Macrophthalmus japonicus	1, 5	2, 2 (4)	1, 1, 6	0	–	Aikawa, 1929
Macrophthalmus sulcatus	1, 5	2, 2 (4)	1, 1, 6	0	–	Hashmi, 1969
Macrophthalmus latreillis	1, 5	2, 2 (4)	0, 1, 6	0	–	Hashmi, 1969
Macrophthalmus pacificus	1, 5	2, 2 (4)	0, 1, 5	0	–	Hashmi, 1969
Macrophthalmus crinitus	1, 4	2, 3 (5)	0, 1, 6	2	+	Hashmi, 1969
Hemiplax hirtipes	1, 5	2, 2 (4)	0, 1, 6	0	+	Wear, 1968
OCYPODINAE						
Ocypode quadrata	0, 5	1, 2 (3)	0, 0, 5	0	+	Diaz & Costlow, 1972
Ocypode platytarsis	—	1, 2 (3)	0, 0, 4	0	+	Rajabai, 1951
Ocypode gaudichaudii	0, 4	1, 2 (3)	0, 0, 5	0	+	Crane, 1940
Uca annulipes	0, 4	1, 2 (3)	0, 0, 4	0	–	Feest, 1969
Uca annulipes	0, 4	1, 2 (3)	0, 0, 4	1	–	Hashmi, 1968
Uca marionis	0, 4	1, 2 (3)	0, 0, 5	0	–	Hashmi, 1968
Uca pugilator	0, 4	1, 2 (3)	0, 0, 4	0	–	Hyman, 1920
Uca pugnax	0, 4	1, 2 (3)	0, 0, 4	0	–	Hyman, 1920
Uca minax	0, 4	1, 2 (3)	0, 0, 4	0	–	Hyman, 1920
Uca triangularis	0, 4	1, 2 (3)	0, 0, 4	0	–	Feest, 1969
SCOPIMERINAE						
Scopimera globosus	0, 5	2, 3 (5)	0, 1, 6	0	+	Aikawa, 1929
Dotilla sulcata	0, 4	2, 3 (5)	—	0	+	Gohar & Al-Kholy, 1957
Dotilla sulcata	0, 4	2, 2 (4)	0, 2, 4	0	+	Ramadan, 1940
Dotilla blanfordi	0, 4	2, 3 (5)	1, 1, 4	0	–	Rajabai, 1959
Ilyoplax pusillus	0, 4	2, 3 (5)	1, 1, 5	0	+	Aikawa, 1929
Ilyoplax gangetica	0, 4	(4–5)	0, 5	0	–	Feest, 1969
MICTYRIDAE ?						
Mictyris longicarpus	1, 5	2, 2 (4)	1, 1, 6	0	–	Cameron, 1965

Thus the zoeae of the genera *Macrophthalmus* and *Hemiplax* (sub-family Macrophthalminae) all have the basal segment of the endopod of the maxillule armed with a single seta, the endopod of the maxilla armed with a total of four or five setae, and the middle segment of the endopod of the second maxilliped carrying a single seta. In contrast, the genera *Ocypoda* and *Uca* (sub-family Ocypodinae) have both the basal segment of the endopod of the maxillule and the middle segment of the endopod of the second maxilliped unarmed, while the endopod of the maxilla carries a total of only three setae. Larvae of the third sub-family, the Scopimerinae, represented by the genera *Scopimera*, *Ilyoplax* and *Dotilla*, show a combination of these characters which tend to exclude them from both of the other two groups. Finally, the first zoea of *Mictyris longicarpus* Latreille has setal characters similar to those of the Macrophthalminae but, as pointed out by Wear (1968), it possesses other characters, including the absence of both dorsal and lateral carapace spines and the form of the telson, which may support Balss' (1957) separation of *Mictyris* into a distinct family.

Table 1 also includes data on the armature of the telson forks and the presence or absence of lateral caparace spines, showing that these characters are not correlated with the sub-family groups but vary even within the same genus.

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